ÖGH Herpetozoa
Austrian Herpetological Society

Herpetozoa 38: 191–204 (2025)
DOI 10.3897/herpetozoa.38.e151017

Ecological niches and climate-driven range shifts in *Hemorrhois* snakes: implications for biogeography

Mehmet Kürşat Şahin[1]

1 *Department of Biology, Faculty of Science, Hacettepe University, 06800 Ankara, Turkiye*

https://zoobank.org/996523A6-FF0D-43C5-BEB8-5CEA449233C7

Corresponding author: Mehmet Kürşat Şahin (kursat.sahin@hacettepe.edu.tr)

Academic editor: Yurii Kornilev ♦ **Received** 21 February 2025 ♦ **Accepted** 21 July 2025 ♦ **Published** 6 August 2025

Abstract

Understanding the factors shaping species distributions is essential for predicting their responses to environmental change. The genus *Hemorrhois* (horseshoe whip snakes) comprises ecologically diverse colubrid snakes found across the Mediterranean Basin, North Africa, the Middle East, and Central Asia. Despite this broad range, their ecological niches and distributional dynamics remain understudied. This study employs ecological niche modeling (ENM) to assess the biogeography, niche differentiation, and potential climate-driven range shifts of *H. algirus*, *H. hippocrepis*, *H. nummifer*, and *H. ravergieri* under future climate scenarios. Using species occurrence data and bioclimatic variables, I constructed ensemble models to predict suitable habitats, evaluate niche overlap, and quantify potential range changes. Results indicate significant variation in climate-driven distributional responses among species. *Hemorrhois algirus* is projected to expand across North Africa, whereas *H. hippocrepis*, *H. nummifer*, and *H. ravergieri* may face range contractions under high-emission scenarios. Niche analyses suggest moderate overlap between *H. algirus* and *H. hippocrepis*, implying historical and ecological connectivity, while *H. nummifer* and *H. ravergieri* display distinct environmental preferences. Climatic and geographic barriers—such as the Sahara Desert, the Dardanelles and Istanbul Straits, the Alps, and the Pyrenees Mountains—play crucial roles in shaping their evolutionary trajectories. Given the increasing threats of climate change and habitat loss, this study underscores the need for conservation strategies prioritizing habitat connectivity, species-specific management, and climate refugia. By integrating ecological and evolutionary perspectives, this research contributes to understanding Mediterranean and Western Palearctic reptile biogeography and their responses to environmental change.

Key Words

climate change, habitat loss, niche differentiation, Squamata, Western Palearctic

Introduction

Species distributions and their ecological niches are shaped by a combination of historical biological and geological events, climatic fluctuations, and biotic interactions (Franklin 2009). Continental drift, glaciations, and environmental shifts have profoundly influenced present-day biodiversity by driving speciation and dispersal (Wiens 2011; Pelegrin et al. 2021). Within these frameworks, interspecific competition, environmental pressures, and selective forces further shape evolutionary trajectories (Angert and Schemske 2005; Sexton et al. 2009). Understanding the processes governing species' ecological niches is critical for predicting their responses to environmental change and informing conservation efforts (Soberon and Peterson 2005; Franklin 2009; Vaissi and Mohammadi 2024).

Climate change represents a significant threat to many reptilian taxa, particularly those with narrow ecological tolerances or fragmented distributions (Vaissi et al. 2023; Şahin 2024). Recent advances in ecological modeling, coupled with global climate and land cover datasets, now allow researchers to forecast species distributions under different environmental scenarios. Ecological niche models (ENMs) integrate occurrence data and environmental variables to

Copyright *Mehmet Kürşat Şahin*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

predict potential species range shifts under climate change (Phillips and Dudík 2008; Peterson et al. 2011). However, significant conceptual and statistical challenges exist in niche modeling using occurrence records that encompass a geographically representative range of species. For example, most ENMs exhibit spatial correlation among environmental variables, such as temperature, which may lead to misinterpretation of significant niche modeling results as a consequence of geographical distance (McCormack et al. 2010).

The genus *Hemorrhois* (Colubridae), commonly referred to as the horseshoe whip snakes, comprises four currently recognized species: *Hemorrhois algirus*, *H. hippocrepis*, *H. nummifer*, and *H. ravergieri* (Abreu 2017; Faraone et al. 2020; Kazemi et al. 2023). This genus exhibits a broad yet regionally distinct distribution, primarily spanning the Mediterranean Basin, North Africa, the Middle East, and parts of Central and South Asia (Carranza et al. 2006; Abreu 2017; Bülbül et al. 2019; Faraone et al. 2020). *Hemorrhois* snakes display notable ecological adaptability, occupying diverse habitats including arid and semi-arid landscapes, rocky terrains, and anthropogenically modified environments (Montes et al. 2020). The broad distribution and ecological plasticity of *Hemorrhois* make this genus an ideal model system for testing biogeographic and ecological hypotheses. Such studies could elucidate how ecological niches and climate-driven range shifts have shaped their current distributions while also providing insights into potential future range dynamics under contemporary climate change scenarios (Winter et al. 2016; Veverková 2021).

Despite their broad distributions, *Hemorrhois* snakes generally remain relatively understudied with regard to their ecological interactions and responses to environmental changes. The integration of species distribution modeling and niche differentiation assessments will clarify the role of climate in their speciation and habitat requirements for conservation planning. Given the increasing pressures of habitat destruction and climate change, future research should prioritize identifying key refugia, assessing population viability, and implementing conservation strategies that account for both regional and global threats to these snakes (Bombi et al. 2011).

This study provides a comprehensive assessment of the biogeography and ecological niches of the genus *Hemorrhois* by integrating occurrence records, climatic variables, and predictive modeling techniques. I hypothesize that *Hemorrhois* species exhibit significant climatic niche differentiation corresponding to their ecological and biogeographic diversity and that climate change will drive species-specific range shifts. To test this hypothesis, I developed ENMs based on climatic variables and species occurrence data to (i) evaluate the relationship between current *Hemorrhois* distributions and observed climate and forecast potential future species distributions under different climate change scenarios (2081–2100) and (ii) measure and compare climatic niche divergence within the genus. These findings will contribute to a better understanding of Mediterranean and Palearctic reptile biogeography and offer insights into the resilience and adaptability of *Hemorrhois* species in the face of ongoing environmental transformations.

Materials and methods

Study area and species occurrences

The study area encompasses the entire distributional range of *Hemorrhois* (20°W to 80°E longitude, 25° to 48°N latitude), spanning diverse ecosystems across Southern Europe (including the Iberian Peninsula), North Africa, the Middle East, and Central and Southwestern Asia (Fig. 1). This comprehensive coverage captures the full spectrum of ecological conditions inhabited by the

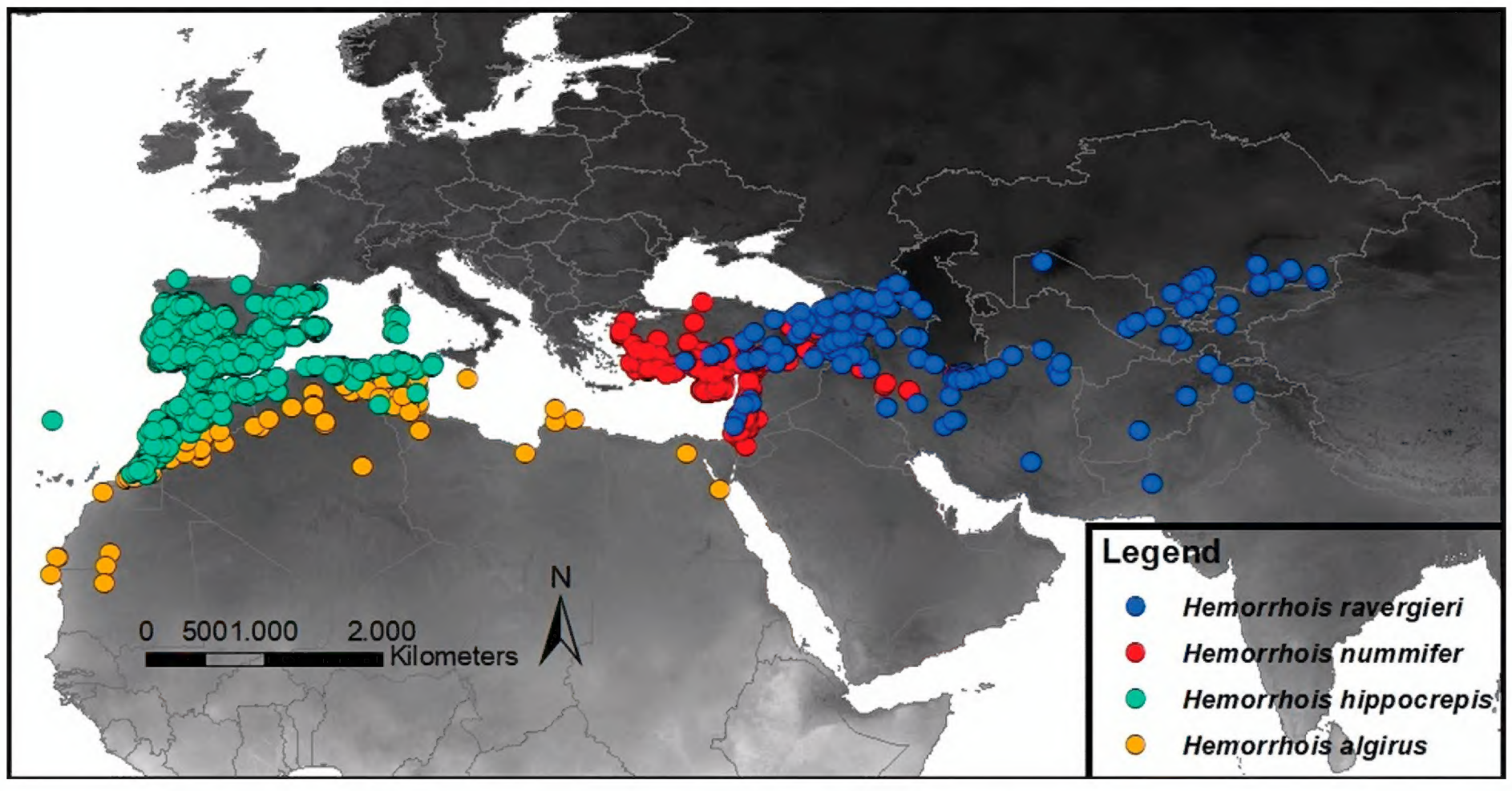

Figure 1. Species occurrence records for genus *Hemorrhois* in Asia, the Middle East, Southern Europe, and North Africa.

genus, enabling robust characterization of their niche preferences. Occurrence records for *Hemorrhois* species were sourced from multiple repositories, including herpetological literature, personal observation data, and online platforms (see Suppl. material 1). The data underwent a two-step process for cleaning and validation to ensure quality and accuracy. The georeferenced occurrence data were systematically analyzed to identify and correct errors and inconsistencies. Initially, I screened the data's geographic accuracy. Records with fewer than three decimal places in their coordinates (equivalent to a spatial uncertainty > 100 meters) were flagged for further validation. For each record, the locality description was cross-checked with the mapped coordinates using GIS software (QGIS v. 3.40.4–Bratislava) to ensure consistency (QGIS 2025). Records showing discrepancies between the locality description and geographic position were excluded. For records obtained from online platforms (GBIF 2024; iNaturalist 2025), I prioritized those marked with high location accuracy (<100 m uncertainty) and validated with photographic evidence or detailed observation notes. Furthermore, to ensure temporal consistency with the bioclimatic layers (CHELSA v. 2.1; Karger et al. 2017; baseline period 1970–2000), I primarily included occurrence records collected during or close to this timeframe. Records with uncertain identification, unclear locations, or poor spatial resolution were omitted from the final dataset to maximize data reliability (Chapman 2005). To reduce geographic sampling biases and improve the interpretation of habitat suitability analyses and niche overlap tests, the R package spThin (Aiello-Lammens et al. 2015) was utilized to spatially rarefy the occurrence records for each *Hemorrhois* species. One locality was retained for every 5 km linear distance to maintain a balance between data density and spatial representation. The retained records were as follows: *H. algirus* – 109 from 170; *H. hippocrepis* – 1,071 from 7,992; *H. nummifer* – 239 from 547; and *H. ravergieri* – 161 from 281.

Bioclimatic variables

Bioclimatic variables were obtained from the CHELSA database at a spatial resolution of 30 arc-seconds (Karger et al. 2017; Brun et al. 2022), and all layers were initially clipped to a broad study area covering the Western Palearctic and adjacent regions. To improve model robustness and avoid overprediction, I defined a species-specific calibration area (M) for each *Hemorrhois* species, following recommendations from ecological niche modeling theory (Soberon and Peterson 2005; Barve et al. 2011; Luna et al. 2024). These M areas were delineated based on each species' known geographic distribution, major dispersal barriers, and regional biogeographical boundaries. Environmental layers were masked to each species' M area prior to modeling, ensuring that pseudo-absences and background data were sampled only from regions ecologically accessible to the species. This strategy reduces model bias and improves the reliability of post-modeling analyses such as niche overlap and divergence (Araújo and New 2007; Phillips et al. 2009; Luna et al. 2024).

Pearson correlations among variables were computed using R v4.3 (R Core Team 2024), and variables with high correlations ($r \geq |0.8|$) were removed. Eight bioclimatic variables were selected for model construction across all four species: mean diurnal air temperature range (Bio_2), isothermality (Bio_3), temperature seasonality (Bio_4), mean daily maximum air temperature of the warmest month (Bio_5), daily mean air temperatures of the wettest quarter (Bio_8), daily mean air temperatures of the driest quarter (Bio_9), precipitation seasonality (Bio_15), and mean monthly precipitation amount of the warmest quarter (Bio_18); hereafter, the Bio_ codes are used throughout. All variables were applied to forecast species niches under recent (1970–2000) and future (2071–2100) climate change projections using GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL models. These global circulation models were selected based on their optimal performance for the study area, and projections were evaluated under the lowest and highest shared socioeconomic pathways (SSPs) from the Coupled Model Intercomparison Project Phase 6 (CMIP6) (Eyring et al. 2016; Sun et al. 2022).

Ecological niche modeling

An ensemble model was developed to predict the potential suitable habitats of *Hemorrhois* species, utilizing six distinct algorithms: generalized linear model (GLM), generalized additive model (GAM), surface range envelope (SRE/BIOCLIM), domain model (DM), random forest (RF), and maximum entropy (MAXENT). This was implemented using the ENMTools and kuenm packages (Cobos et al. 2019; Warren et al. 2021) in R. The ensemble model represents a proportional aggregation of the responses generated by the algorithms (Table 1). This approach leverages the strengths of these algorithms while reducing their respective weaknesses, enhances accuracy, and offers a quantifiable measure of uncertainty in predictions (Araújo and New 2007). Some of these algorithms require datasets that include both presence and absence data; however, obtaining real absence data is challenging. To minimize potential biases, pseudo-absences were generated using a target-group sampling approach (Phillips et al. 2009). Pseudo-absences were selected based on environmental constraints, ensuring they were located in areas not occupied by the species but within suitable climatic conditions. The models were calibrated using 80% of the data (training set) and assessed using the remaining 20% (validation set). This process was repeated three times to enhance model training coverage and increase robustness.

Table 1. Model comparisons for species distribution of genus *Hemorrhois* according to AUC values.

Species	GLM	GAM	RF	DM	BC	MaxEnt
H. algirus	0.847	0.861	0.903	0.873	0.864	0.955
H. hippocrepis	0.861	0.829	0.888	0.851	0.910	0.943
H. nummifer	0.865	0.868	0.922	0.899	0.898	0.959
H. ravergieri	0.805	0.811	0.813	0.804	0.810	0.915

*GLM: General linear model, GAM: General Additive Model, RF: Random Forest, DM: Domain Model, BC: Bioclim, MaxEnt: Maximum Entropy.

Model selection

To ensure optimal model complexity, 341 candidate MAXENT models were tested using combinations of feature classes (hinge, threshold, product, quadratic, and linear) and regularization multipliers (ranging from 0.1 to 10). Feature class selection was based on previous studies demonstrating their role in controlling model complexity and preventing overfitting (Muscarella et al. 2014; Cobos et al. 2019). Regularization multipliers were adjusted to balance model generality and complexity, ensuring biologically meaningful predictions (Radosavljevic and Anderson 2014). The application of these combinations provided an optimal strategy for generating diverse candidate models, enabling the selection of those that best explained the data.

Subsequently, the 341 candidate MAXENT models were evaluated using a multi-criteria assessment framework. Optimal models were selected based on (i) the highest Area Under the Curve (AUC) values, (ii) the lowest Akaike Information Criterion corrected for small sample sizes (AICc) (Hurvich and Tsai 1989), (iii) statistical significance based on partial ROC (pROC) tests (Peterson et al. 2008), and (iv) a predictive omission rate threshold set at 5% (Table 2) (Anderson et al. 2003). This combination of independent metrics offers a comprehensive and robust assessment of model performance and reliability, reducing the risk of overfitting and ensuring that selected models reflect both statistical and ecological relevance (Araújo and New 2007). AUC values were interpreted as follows: AUC = 0.5 indicates random prediction, AUC > 0.7 suggests useful performance, > 0.8 is satisfactory, and > 0.9 is excellent (Manel et al. 2001; Adhikari et al. 2018; Li et al. 2024). By integrating these complementary evaluation methods, the final models were both statistically robust and ecologically meaningful. Projections for the recent period were generated using the optimal configuration of the statistical model, utilizing 100% of the records and conducting 5,000 iterations with 10 replicates. All model outputs were ultimately converted into binary predictions using the minimum training presence threshold to distinguish between unsuitable and suitable areas (Pearson 2007; Rodríguez-Ruiz et al. 2020). Future projections were performed using climate layers from five general circulation models (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL) under two shared socioeconomic pathways (SSP126 and SSP585). During model transfer to future conditions, extrapolation was permitted but carefully constrained based on model response curves to avoid biologically implausible projections (Owens et al. 2013; Gomes et al. 2018). To assess and quantify areas of strict extrapolation—where environmental conditions differ substantially from those of the calibration region—a Mobility-Oriented Parity (MOP) analysis was conducted using the *new MOP* package (Cobos et al. 2024). MOP results were used to identify regions of higher uncertainty in future projections, and interpretations of range shifts were made cautiously, taking these uncertainty zones into account (Suppl. materials 2–5). The contributions of the bioclimatic variables are presented in Table 3. Median values from the replicates were used to summarize model predictions for each climate scenario (Figs 2–5).

Species range change

To assess and visualize potential species range change (SRC) in *Hemorrhois* species under climate change scenarios, a spatial analysis approach was employed to generate maps depicting regions where species may experience gains or losses in suitable conditions. The metrics include "Loss" (the number of pixels anticipated to become unsuitable), "Absent" (the number of pixels expected to remain unsuitable), "Stable" (the number of pixels projected to remain suitable), and "Gain" (the number of pixels predicted to become suitable). These estimates are based on model predictions and do not directly represent the species' actual area of occupancy, as they are derived from binarized model outputs using a specified threshold (Guisan et al. 2018). In addition to absolute measures, three relative

Table 2. Summary statistics for the best models selected for species distribution maps of *Hemorrhois* species.

Species	Feature	Candidate models	Statistically significant models	Mean AUC ratio	Partial ROC	Omission rate at 5%	AICc	ΔAICc	W AICc	AUC
H. algirus	product + threshold	341	340	1.741	0	0.044	2891.214	0	0.914	0.955
H. hippocrepis	quadratic+ product	341	36	1.873	0	0.049	2893.732	0	1	0.943
H. nummifer	linear + threshold	341	175	1.729	0	0.039	6643.085	0	0.718	0.959
H. ravergieri	product	341	341	1.420	0	0.090	4873.719	0	1	0.915

AICc: a corrected AIC score, used for a small sample size by increasing the cost for each parameter; wAICc: the model weight is the relative likelihood for each model divided by the total relative likelihood for all models that were considered. ΔAICc: the difference between the model with the lowest score (the "best" model) and the AICc score for each model; AUC: area under the curve is a measure of the accuracy of the model; mean AUC ratio ≥ 1.00, $p < 0.05$ means predictions are significantly better than a random model.

Table 3. Contributions of bioclimatic variables.

Species / Variable %	Bio 2	Bio 3	Bio 4	Bio 5	Bio 8	Bio 9	Bio 15	Bio 18
H. algirus	5.1	31.9	15.5	0.9	4.4	3.7	7.1	31.4
H. hippocrepis	11.5	15.4	29.8	4.3	1.9	2.7	16.7	17.7
H. nummifer	15.6	0.8	11.9	7.7	19.5	6.8	25.1	12.6
H. ravergieri	13.9	4.1	34.1	18.3	5.5	4.1	4.8	15.2

metrics were developed to clarify the potential effects of climate change on the distributions of *Hemorrhois* species (Table 4; Suppl. material 6):

1. Percentage Loss: the proportion of currently occupied sites anticipated to be lost. Calculated as: Loss / (Loss + Stable).
2. Percentage Gain: the ratio of new sites anticipated for the species relative to its existing distribution size. Calculated as: Gain / (Loss + Stable).
3. Range Change: the net alteration in the species' range size, accounting for both gains and losses. Calculated as: Percentage Gain – Percentage Loss.

These metrics provide important insights into the potential impacts of climate change on the distribution of *Hemorrhois* species. The analysis of these metrics across different climate scenarios enables a thorough understanding of potential range shifts for each species (Guisan et al. 2018).

Niche analysis

To evaluate ecological niche differentiation among *Hemorrhois* species, I implemented a comprehensive analytical framework combining traditional overlap metrics with multivariate statistical techniques. First, I calculated Schoener's D (difference-focused) and Hellinger's I (similarity-focused) indices to quantify niche similarity, with values ranging from 0 (no overlap) to 1 (identical niches) (Warren et al. 2021). Subsequently, a multivariate analysis of variance (MANOVA) was conducted to assess whether the environmental conditions occupied by each species differed significantly. To further validate the results of the niche overlap analyses, background similarity tests were performed using a Monte Carlo randomization approach with 500 replicates, comparing observed niche overlap metrics (Schoener's D and Hellinger's I) against a null distribution of randomized backgrounds (Warren et al. 2021) (Suppl. material 7). This higher number of replicates ensured a more stable and reliable estimation of null distributions, allowing for robust significance testing (Table 5; Suppl. material 8). Although climate variables are primary drivers of niche differentiation (e.g., competitive exclusion), habitat partitioning may further constrain species distributions. It is therefore essential to understand whether ecological niches remain conserved or diverge over evolutionary time. Niche conservatism refers

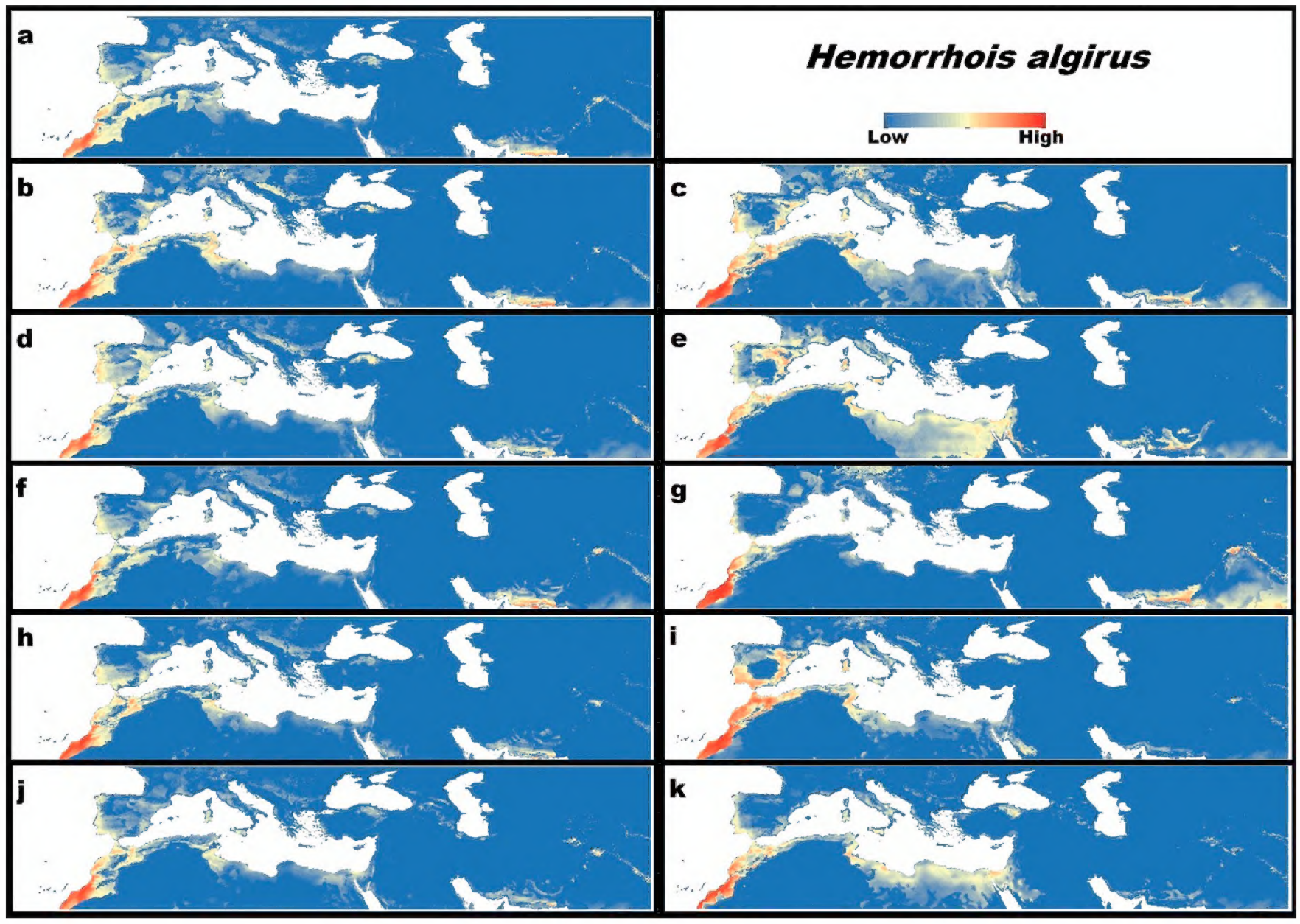

Figure 2. Recent (1970–2000) and future (2081–2100) climatic suitability for *Hemorrhois algirus* based on different models under the optimistic (ssp126) and pessimistic (ssp585) scenarios. (**a.** Recent; **b.** GFDL 126; **c.** GFDL 585; **d.** IPSL 126; **e.** IPSL 585; **f.** MPI 126; **g.** MPI 585; **h.** MRI 126; **i.** MRI 585; **j.** UKESM 126; **k.** UKESM 585).

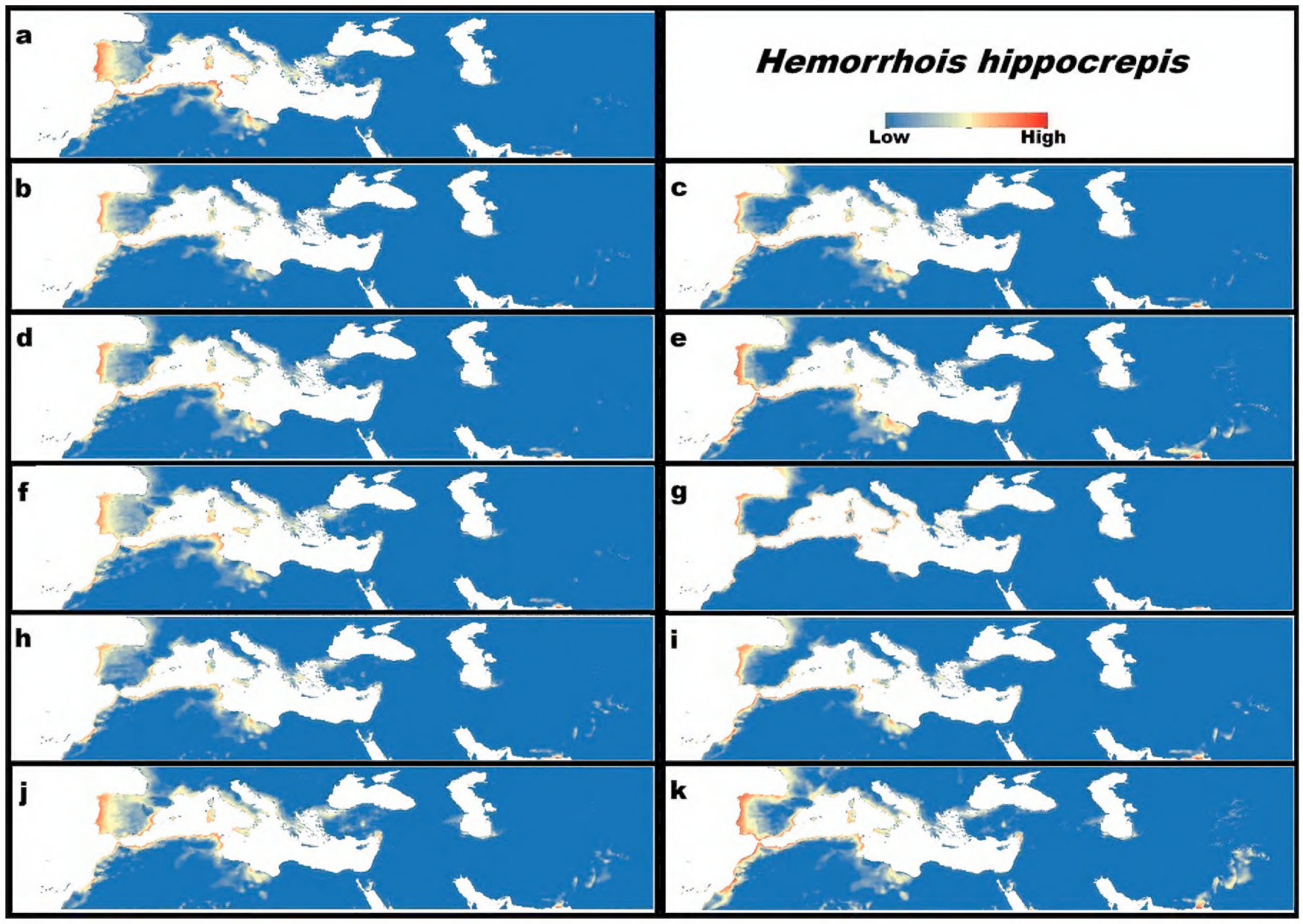

Figure 3. Recent (1970–2000) and future (2081–2100) climatic suitability for *Hemorrhois hippocrepis* based on different models under the optimistic (ssp126) and pessimistic (ssp585) scenarios. (**a.** Recent; **b.** GFDL 126; **c.** GFDL 585; **d.** IPSL 126; **e.** IPSL 585; **f.** MPI 126; **g.** MPI 585; **h.** MRI 126; **i.** MRI 585; **j.** UKESM 126; **k.** UKESM 585).

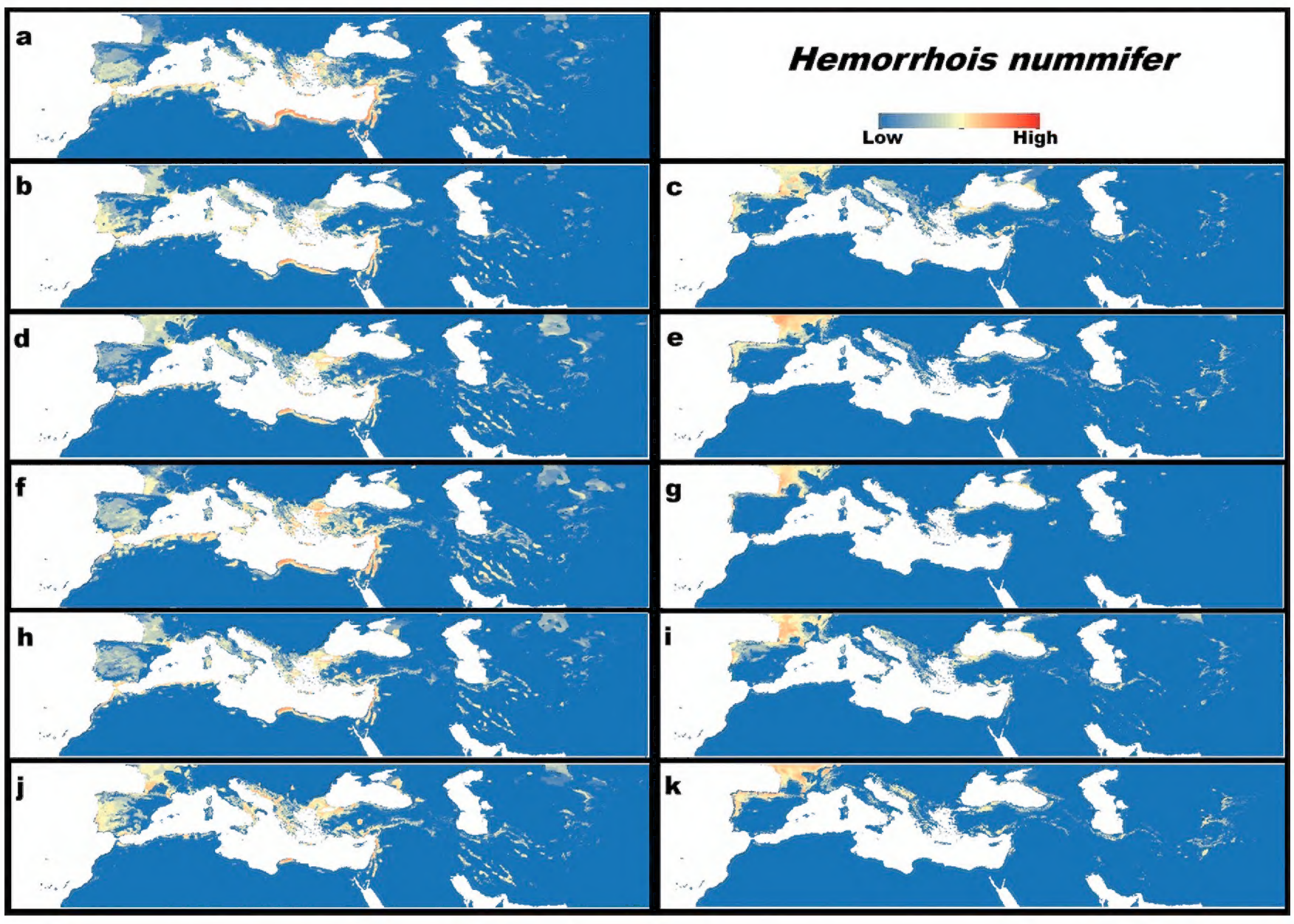

Figure 4. Recent (1970–2000) and future (2081–2100) climatic suitability for *Hemorrhois nummifer* based on different models under the optimistic (ssp126) and pessimistic (ssp585) scenarios. (**a.** Recent; **b.** GFDL 126; **c.** GFDL 585; **d.** IPSL 126; **e.** IPSL 585; **f.** MPI 126; **g.** MPI 585; **h.** MRI 126; **i.** MRI 585; **j.** UKESM 126; **k.** UKESM 585).

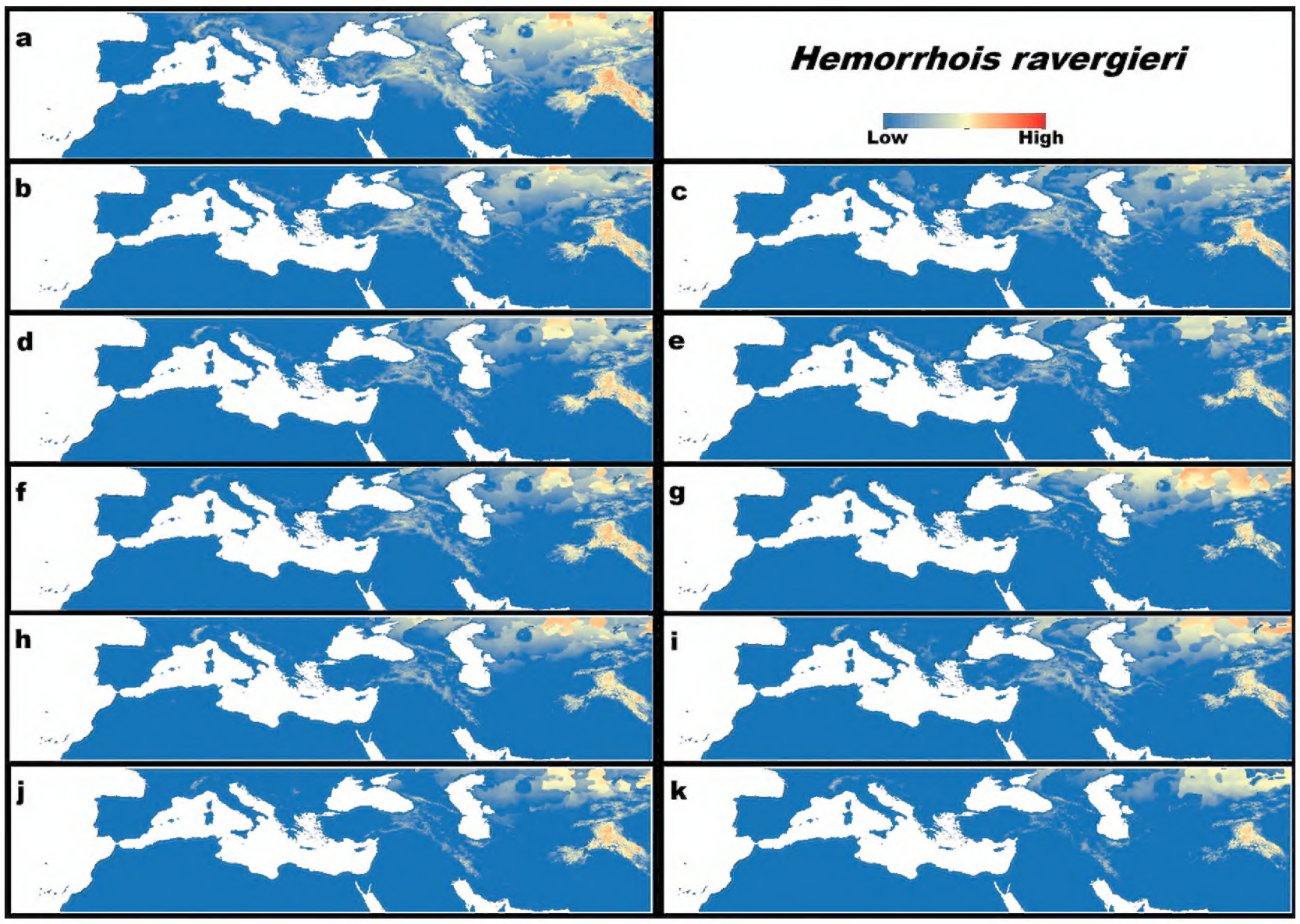

Figure 5. Recent (1970–2000) and future (2081–2100) climatic suitability for *Hemorrhois ravergieri* based on different models under the optimistic (ssp126) and pessimistic (ssp585) scenarios. (**a.** Recent; **b.** GFDL 126; **c.** GFDL 585; **d.** IPSL 126; **e.** IPSL 585; **f.** MPI 126; **g.** MPI 585; **h.** MRI 126; **i.** MRI 585; **j.** UKESM 126; **k.** UKESM 585).

Table 4. Species range change (SRC) of *Hemorrhois* species in recently suitable habitats (gain/loss) by 2081–2100 under optimistic (ssp126) and pessimistic (ssp585) scenarios.

Species	Models	ssp 126			ssp 585		
		Loss%	Gain%	SRC	Loss%	Gain%	SRC
H. algirus	GFDL	24.835	51.704	26.869	37.479	87.835	50.356
	IPSL	25.452	57.618	32.166	55.364	74.289	18.925
	MPI	16.785	39.717	22.932	66.008	52.168	-13.840
	MRI	30.486	39.004	8.518	56.218	66.134	9.916
	UKESM	25.435	47.649	22.214	58.336	69.940	11.604
H. hippocrepis	GFDL	29.754	7.031	-22.723	33.283	14.912	-18.371
	IPSL	13.709	9.614	-4.095	36.498	21.176	-15.322
	MPI	4.987	16.539	11.552	79.754	9.542	-70.212
	MRI	17.442	12.587	-4.855	42.728	14.378	-28.350
	UKESM	9.604	35.054	25.450	23.948	45.717	21.769
H. nummifer	GFDL	48.962	12.032	-36.930	93.914	26.065	-67.849
	IPSL	42.159	21.548	-20.611	95.113	23.581	-71.532
	MPI	20.834	25.842	5.008	97.441	9.971	-87.470
	MRI	42.659	18.103	-24.556	89.894	24.405	-65.489
	UKESM	57.535	21.942	-35.593	96.142	25.915	-70.227
H. ravergieri	GFDL	3.394	7.071	3.677	9.207	6.996	-2.211
	IPSL	8.979	3.204	-5.775	20.203	6.109	-14.094
	MPI	8.814	1.554	-7.260	43.978	1.839	-42.139
	MRI	13.606	4.423	-9.183	10.183	8.210	-1.973
	UKESM	32.516	0.716	-31.800	40.609	1.086	-39.523

Table 5. Identity and Background Tests for genus *Hemorrhois*.

Hemorrhois comparisons	Identity test				Background test (asymmetric)				Background test (symmetric)			
	D_0	D_1	I_0	I_1	D_0	D_1	I_0	I_1	D_0	D_1	I_0	I_1
algirus vs. hippocrepis	0.429	0.830	0.716	0.976	0.454	0.674	0.744	0.901	0.446	0.689	0.728	0.898
algirus vs. nummifer	0.275	0.727	0.551	0.918	-	-	-	-	-	-	-	-
algirus vs. ravergieri	0.290	0.843	0.565	0.978	-	-	-	-	-	-	-	-
hippocrepis vs. nummifer	0.273	0.854	0.567	0.969	-	-	-	-	-	-	-	-
hippocrepis vs. ravergieri	0.387	0.833	0.672	0.978	-	-	-	-	-	-	-	-
nummifer vs. ravergieri	0.560	0.870	0.833	0.985	0.578	0.582	0.853	0.846	0.563	0.584	0.819	0.807

to the tendency of species to retain ancestral ecological traits, while niche divergence implies adaptation to different environmental conditions. By integrating statistical validation with ecological interpretation, this study provides a comprehensive framework for understanding niche dynamics in *Hemorrhois*.

Results

Ecological niche models predicted distinct environmental suitability patterns among *Hemorrhois* species, with consistent outputs across algorithms. The performance evaluation of the models—based on AUC, AICc, partial ROC, and omission rates—indicated that all selected models demonstrated high predictive accuracy and statistical significance, supporting their reliability for subsequent analyses (Tables 1, 2). The regions projected to be suitable for *Hemorrhois* species demonstrated significant model performance: *H. algirus* (AUC = 0.955, omission rate at 5% = 0.044), *H. hippocrepis* (AUC = 0.943, omission rate at 5% = 0.049), *H. nummifer* (AUC = 0.959, omission rate at 5% = 0.039), and *H. ravergieri* (AUC = 0.915, omission rate at 5% = 0.090). Although several statistically significant models were identified for each *Hemorrhois* species, only one per species met the AICc criterion of ≤ 2. The relative contributions of bioclimatic variables to the ecological niche models of *Hemorrhois* species are summarized in Table 3.

Model projections under future climate scenarios suggest heterogeneous responses among *Hemorrhois* species, with some showing potential range expansions, others contractions, and a few maintaining relatively stable distributions (Figs 2–5). Projected patterns of range stability, expansion, and contraction for each *Hemorrhois* species are summarized in Suppl. material 6 and Table 4. The following results describe species-specific responses of *Hemorrhois* taxa to future climate scenarios, highlighting patterns of range expansion, contraction, and stability.

For *H. algirus*, Bio_3 (31.9%) and Bio_18 (31.4%) were the two most important variables affecting its potential distribution (Table 3). The habitat suitability map under recent climatic conditions indicates that North Africa—particularly Morocco and northern Algeria—has high suitability (Fig. 2a). While the species occurs in arid environments such as Tunisia and Western Sahara, it is projected to occupy these regions with relatively limited suitable habitat (Fig. 2b–k). In the future, the distribution range of *H. algirus* may expand further in North Africa. For example, under the SSP585 scenario, the GFDL (Fig. 2c) and IPSL (Fig. 2e) models predict range expansions of approximately 50.3% and 18.9%, respectively, compared to the current distribution (Table 4). Based on the SRC analysis, range expansion is expected under all optimistic and pessimistic future climate scenarios, except for MPI SSP585 (–13.8%) (Suppl. material 6: fig. S5A).

For *H. hippocrepis*, Bio_4 (29.8%) and Bio_18 (17.7%) were identified as the most influential variables shaping its potential distribution (Table 3). The habitat suitability map under current climatic conditions indicates a broad and continuous distribution across southern Europe and the western Mediterranean coast. In particular, the Iberian Peninsula (Spain and Portugal) and parts of Italy exhibit high suitability (Fig. 3a). The species shows a notable preference for coastal regions over inland areas (Fig. 3b–k). In the future, a significant range contraction is projected under high-emission scenarios. For instance, under the SSP585 scenario in the MPI model, a loss of approximately 70.2% of suitable habitat is predicted within the species' current distribution range (Fig. 3g, Table 4). SRC analysis further supports this trend, indicating range contraction under all future climate scenarios—except expansions in MPI SSP126 (11.5%) and both UKESM scenarios (25.4% under SSP126 and 21.7% under SSP585) (Suppl. material 6: fig. S5B).

For *H. nummifer*, Bio_15 (25.1%) and Bio_8 (19.5%) were the most influential variables contributing to its potential distribution (Table 3). The habitat suitability map under current climatic conditions shows a wide distribution primarily across the Levantine corridor, extending into parts of western Anatolia and the Middle East (Fig. 4a). This pattern suggests adaptation to semi-arid and Mediterranean environments. Under future climate scenarios, a notable range contraction is projected, particularly under high-emission conditions. For example, under the SSP585 scenario, the MPI model predicts a loss of approximately 87.4% of suitable habitat, especially in surrounding countries of the Levantine corridor and western Anatolia (Fig. 4f, Table 4). According to the SRC analysis, habitat loss is expected under nearly all future scenarios—specifically 4 out of 5 under SSP126 and all 5 models under SSP585—except for MPI SSP126, which predicts a limited expansion (5%) (Suppl. material 6: fig. S5C).

For *H. ravergieri*, Bio_4 (34.1%) and Bio_5 (18.3%) were the most influential variables shaping its potential distribution (Table 3). The habitat suitability map under current climatic conditions highlights high suitability across South-Central Asia—particularly northwestern Kazakhstan and Mongolia—as well as western Asia (Türkiye) and the Caucasus region (Fig. 5a). In future climate scenarios, areas at higher elevations are projected to become increasingly suitable (Fig. 5b–k). However, under the SSP585 scenario, both the MPI and UKESM models predict notable range contractions, with losses of 42.1% and 39.5% of suitable habitat, respectively, particularly in the Caucasus and western Asia (Table 4, Suppl. material 6: fig. S5D).

The comparative analysis of range shift patterns among *Hemorrhois* species revealed contrasting responses to projected climate change. *Hemorrhois algirus* is generally expected to expand its suitable range across North Africa, while *H. hippocrepis*, *H. nummifer*, and *H. ravergieri* are projected to experience significant range contractions under pessimistic climate scenarios. The degree of projected range loss was highest for *H. nummifer* and *H. ravergieri*, particularly in regions of complex topography and aridification, suggesting species-specific sensitivity to climatic variables and geographic constraints.

The measured niche overlaps among all species are presented in Table 5. The null hypothesis regarding niche overlap among *Hemorrhois* species (excluding *nummifer* vs. *ravergieri* and *hippocrepis* vs. *algirus*) was rejected, as the empirical values for Schoener's D and Hellinger's I test statistics differed significantly from the null distribution of overlap tests for each species comparison (Suppl. material 7: fig. S6A–F) (t test, df = 99, $P < 0.05$). The ecological niche models of the majority of these species were not equivalent. The asymmetric and symmetric background tests for the parapatric *H. algirus* and *H. hippocrepis*, as well as *H. nummifer* and *H. ravergieri*, confirmed partial niche overlap between these species with respect to global bioclimatic variables (Suppl. material 8: fig. S7A–D).

Discussion

This study provides a comprehensive examination of the ecological niche attributes and future range dynamics of four *Hemorrhois* species. The biogeographical patterns of these species are influenced by both historical and contemporary ecological processes. The presence of *H. hippocrepis* in the western Mediterranean, for instance, suggests a complex history of dispersal and vicariance events (Bombi et al. 2011). Specifically, physical barriers such as the Sahara Desert, the Alps, the Pyrenees, and the Dardanelles and Istanbul straits have historically limited gene flow and contributed to speciation through allopatric divergence (Machado et al. 2021). The initial divergence between *H. algirus* and *H. hippocrepis* has been estimated to have occurred during the late Miocene to early Pliocene, approximately 4–7 million years ago (Carranza et al. 2006). Subsequent climatic events during the Pleistocene, including sea-level fluctuations at the Strait of Gibraltar, likely influenced the secondary contact, distributional shifts, or population structure of *Hemorrhois* species. Based on current distributions and phylogenetic inference, *H. algirus* and *H. hippocrepis* may have originated in North Africa, with *H. hippocrepis* subsequently dispersing into the Iberian Peninsula (Carranza et al. 2006). Instead of direct transmarine migration following the opening of the Strait of Gibraltar at the end of the Messinian, climatic events during the Pleistocene glaciations resulted in a sea-level drop of approximately 130 m (Anderson and Borns Jr. 1997) at Camarinal Sill, where water depths range from 40 to 150 m (Brandt et al. 1996). Consequently, some elevated areas in this region temporarily became small islands, potentially allowing certain terrestrial vertebrates—such as the snakes examined here—to traverse the Strait of Gibraltar relatively recently (Carranza et al. 2006). In addition, the Alps (Central Europe) and Pyrenees (between France and Spain) may act as major dispersal barriers due to their cold temperatures, steep terrain, and limited prey availability for *H. hippocrepis*, which prefers lower elevations with stable temperatures. High-altitude mountain zones often present unsuitable conditions (e.g., frost, low prey density) (Pleguezuelos and Feriche 2002). These findings suggest that climatic conditions and geographic features may have significantly shaped the historical distributions of *Hemorrhois* species in the region. Notably, physical barriers such as the Dardanelles and Istanbul straits to the north—and the Sahara Desert to the south—could have influenced dispersal and population structure, especially for *H. nummifer* and *H. ravergieri*. The Sahara, with its extreme heat, scarce water, and limited prey, likely served as an inhospitable barrier. Likewise, although the Dardanelles and Istanbul straits are narrow, they probably acted as persistent water barriers between Europe and Asia, restricting gene flow in low-dispersal species—particularly given the absence of land bridges during glaciations, unlike the Strait of Gibraltar. Importantly, similar patterns have been documented in other colubrid snakes. For example, the dice snake (*Natrix tessellata*) exhibits ancestral area reconstruction findings indicating that deserts and mountain corridors in Central Asia and Anatolia significantly shaped lineage distributions (beginning ~3.7 Ma), with Pleistocene glacial refugia emerging as key range modifiers (Salvi et al. 2018; Liz et al. 2021; Romero-Iraola et al. 2023; Jablonski et al. 2024). This supports the idea that both climatic events and geographic barriers have historically constrained colubrid dispersal. Incorporating a similar ancestral-area framework for *Hemorrhois* could further substantiate these biogeographic inferences. Consequently, the current distribution patterns of *Hemorrhois* may also result from allopatric speciation influenced by vicariance, wherein physical barriers caused the separation and divergence of populations.

These contrasting responses to climate change may reflect differences in environmental plasticity, which influence each species' ability to tolerate or adapt to changing conditions. Species occupying broader climatic niches (*H. algirus*) are more resilient, while those reliant on mesic or montane habitats (*H. nummifer*, *H. ravergieri*) show heightened vulnerability. Insular and coastal specialists (*H. hippocrepis*) are additionally constrained by limited dispersal options. These findings highlight that ecological generalists may fare better under climate change, whereas specialists are at greater risk.

Hemorrhois algirus occupies broad arid and semi-arid habitats in North Africa and is projected to expand its range under future climate scenarios. Its adaptation to harsh environmental conditions, along with ecological flexibility, likely confers resilience to increasing temperatures and habitat changes. In contrast, *H. hippocrepis*, which inhabits coastal and insular Mediterranean regions, is expected to experience moderate range contraction. Geographic isolation on islands and shorelines, coupled with limited dispersal ability, may make this species more vulnerable to habitat loss and climate-driven shifts.

Hemorrhois nummifer, distributed across mesic habitats in the Levant, shows the highest projected range contraction. Its dependence on relatively humid conditions renders it particularly sensitive to the aridification trends forecasted under future scenarios. Similarly, *H. ravergieri*,

which occupies montane and steppe habitats in Western and Central Asia, is projected to lose a substantial portion of its range—especially in high-altitude regions, which are disproportionately affected by temperature increases.

These observed patterns are consistent with findings in other reptilian taxa. Genera *Timon* and *Lacerta* exhibit niche conservatism and gradual phenotypic shifts linked to historical climatic stability (Enriquez-Urzelai et al. 2022). Similarly, *Tarentola mauritanica* and genus *Anatololacerta* demonstrate niche divergence and conservatism depending on environmental pressures (Rato et al. 2015; Şahin et al. 2022). Studies on rat snakes (*Zamenis* spp.) revealed both niche divergence and conservatism among lineages (Vaissi et al. 2024). Such comparisons reinforce the generality of the mechanisms driving niche evolution and distributional dynamics observed in *Hemorrhois*.

Given the projections of range contraction for several *Hemorrhois* species, conservation strategies must prioritize habitat connectivity, preservation of climatic refugia, and management of cross-border habitats. Adaptive conservation planning tailored to each species' ecological needs will be crucial. Species like *H. algirus* may benefit from proactive habitat expansion opportunities, whereas *H. nummifer* and *H. ravergieri* will require strategies to mitigate habitat fragmentation and loss.

This study also conducted niche analyses to assess the ecological niche overlap among four *Hemorrhois* species. The results demonstrated a range of niche differentiation—from low to moderate to substantial—reflecting varying degrees of ecological specialization within the genus. The identity and background tests provide insights into niche dynamics, revealing statistical support for niche overlap in only 2 of 8 pairwise comparisons (Table 5; Suppl. materials 7, 8). The comparisons among allopatric *Hemorrhois* species indicated that their niches are not more similar than expected by chance, yet they are not equivalent (Suppl. material 3). Studies on allopatric *Neurergus* species in Anatolia (Gül 2019) and the speciation dynamics of endemic lizards in Madagascar (Nunes et al. 2022) indicate that variations in their climatic niches align with the abiotic environmental conditions of the geographical regions occupied by these allopatric species. Species that are adapted to specific climatic or local conditions experience niche differentiation due to the unique adaptations required for survival and reproduction (Nakazato et al. 2010).

The case of niche overlap in parapatric speciation, as illustrated by the comparisons between *H. hippocrepis* and *H. algirus* and between *H. nummifer* and *H. ravergieri*, requires further discussion due to the restricted distributions of southern Europe and North Africa for *H. hippocrepis* and *H. algirus* and the Eastern Mediterranean and Western Asia for *H. nummifer* and *H. hippocrepis*. The utilization of the niche is significantly influenced by various ecological interactions. Therefore, incorporating data on diverse selective regimes may aid in analyzing the speciation dynamics of these parapatric species (Gavrilets et al. 2000; Mammola et al. 2018).

These findings suggest that, although certain species have established unique ecological niches, a general pattern of niche conservatism is evident within the *Hemorrhois* genus. This tendency toward niche conservatism supports the theory that speciation in *Hemorrhois* may be influenced by the preservation of ancestral ecological features, in line with results reported for other reptile groups (e.g., Morales-Castilla et al. 2011; Pomara et al. 2014; Vaissi et al. 2024).

It is important to interpret these findings with caution, given the inherent limitations of correlative ENMs, which do not incorporate factors such as dispersal constraints, physiological tolerances, or species interactions (Kearney and Porter 2009; Peterson et al. 2015). These limitations underscore the potential value of future research integrating mechanistic or hybrid models.

Conclusion

This study presents a species-level evaluation of ecological niches and projected future distributions for *Hemorrhois* snakes using correlative ecological niche models based on bioclimatic variables. The projections indicate that *H. algirus* may experience range expansion under future climate conditions, whereas *H. nummifer* and *H. ravergieri* are likely to face substantial habitat reductions. These outcomes should be interpreted within the scope of the modeling framework, as correlative ENMs do not incorporate physiological tolerances, dispersal limitations, or biotic interactions. The results suggest that niche differentiation has occurred among species within the genus, with varied ecological preferences likely shaped by historical isolation and climatic gradients. The evolutionary history of *Hemorrhois* species appears to have been influenced by past climatic fluctuations and geographic obstacles such as deserts, mountain systems, and sea barriers. Areas identified as climatically stable under both current and future scenarios may represent important climate refugia that could support long-term population persistence. These findings support the prioritization of such regions in conservation planning and emphasize the need to integrate ecological modeling with physiological, genetic, and dispersal-based approaches in future research.

Acknowledgments

I thank Mr. Hanley Garner for proofreading and Assoc. Prof. Muammer Kurnaz, the respected anonymous reviewers, and the section editor for their valuable suggestions.

References

Abreu JMB (2017) Phylogenetic and diversity patterns of the Algerian whip snake *Hemorrhois algirus*. Master Thesis, University of Porto, Porto, Portugal.

Adhikari P, Shin M-S, Jeon J-Y, Kim HW, Hong S, Seo C (2018) Potential impact of climate change on the species richness of subalpine plant species in the mountain national parks of South Korea. Journal of Ecology and Environment 42: 36. https://doi.org/10.1186/s41610-018-0095-y

Aiello-Lammens ME, Boria RA, Radosavljevic A, Vilela B, Anderson RP (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography 38(5): 541–545. https://doi.org/10.1111/ecog.01132

Anderson BG, Borns Jr HW (1997) The ice age world. An introduction to quaternary history and research with emphasis on North America and Europe during the last 2.5 million years. Scandinavian University Press, Oslo, Norway, 208 pp.

Anderson RP, Lew D, Peterson AT (2003) Evaluating predictive models of species' distributions: Criteria for selecting optimal models. Ecological Modelling 162(3): 211–232. https://doi.org/10.1016/S0304-3800(02)00349-6

Angert AL, Schemske DW (2005) The evolution of species' distributions: Reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. Evolution 59(8): 1671–1684. https://doi.org/10.1111/J.0014-3820.2005.TB01817.X

Araújo MB, New M (2007) Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22(1): 42–47. https://doi.org/10.1016/j.tree.2006.09.010

Boback SM, Nafus MG, Yackel Adams AA, Reed RN (2020) Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities. Ecosphere 11(1): e03000. https://doi.org/10.1002/ecs2.3000

Bombi P, Capula M, D'Amen M, Luiselli L (2011) Climate change threatens the survival of highly endangered Sardinian populations of the snake *Hemorrhois hippocrepis*. Animal Biology 61(3): 239–248. https://doi.org/10.1163/157075511X584191

Brandt P, Alpers W, Backhaus JO (1996) Study of the generation and propagation of internal waves in the Strait of Gibraltar using a numerical model and synthetic aperture radar images of the European ERS 1 satellite. Journal of Geophysical Research: Oceans 101(C6): 14237–14252. https://doi.org/10.1029/96JC00540

Brun P, Zimmermann NE, Hari C, Pellissier L, Karger DN (2022) Global climate-related predictors at kilometer resolution for the past and future. Earth System Science Data 14(12): 5573–5603. https://doi.org/10.5194/essd-14-5573-2022

Bülbül U, Koç H, Bayrak MO, Kutrup B (2019) New locality record and morphological data of *Hemorrhois ravergieri* (Ménétries, 1832) (Serpentes: Colubridae) in Turkey. Turkish Journal of Bioscience and Collections 3(2): 59–62. https://doi.org/10.26650/tjbc.20190005

Carranza S, Arnold EN, Pleguezuelos JM (2006) Phylogeny, biogeography, and evolution of two Mediterranean snakes, *Malpolon monspessulanus* and *Hemorrhois hippocrepis* (Squamata, Colubridae), using mtDNA sequences. Molecular Phylogenetics and Evolution 40(2): 532–546. https://doi.org/10.1016/j.ympev.2006.03.028

Chapman AD (2005) Principles and Methods of Data Cleaning. Primary Species and Species-Occurrence Data, v 1.0. Report for the Global Biodiversity Information Facility, Copenhagen, 75 pp.

Cobos ME, Peterson AT, Barve N, Osorio-Olvera L (2019) kuenm: an R package for detailed development of ecological niche models using Maxent. PeerJ 7: e6281. https://doi.org/10.7717/peerj.6281

Cobos ME, Owens HL, Soberón J, Peterson AT (2024) Detailed multivariate comparisons of environments with mobility oriented parity. Frontiers of Biogeography 17: e132916. https://doi.org/10.21425/fob.17.132916

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists: Statistical explanation of MaxEnt. Diversity and Distributions 17(1): 43–57. https://doi.org/10.1111/j.1472-4642.2010.00725.x

Enriquez-Urzelai U, Martínez-Freiría F, Freitas I, Perera A, Martínez-Solano Í, Salvi D, Velo-Antón G, Kaliontzopoulou A (2022) Allopatric speciation, niche conservatism and gradual phenotypic change in the evolution of European green lizards. Journal of Biogeography 49(12): 2193–2205. https://doi.org/10.1111/jbi.14497

Esparza-Estrada CE, Alencar LRV, Terribile LC, Rojas-Soto O, Yáñez-Arenas C, Villalobos F (2023) Vipers on the Scene: Assessing the Relationship Between Speciation and Climatic Niche Evolution in Venomous Snakes (Reptilia: Viperidae). Evolutionary Biology 50: 264–273. https://doi.org/10.1007/s11692-023-09604-5

Eyring V, Bony S, Meehl GA, Senior CA, Stevens B, Stouffer RJ, Taylor KE (2016) Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. Geoscientific Model Development 9(5): 1937–1958. https://doi.org/10.5194/gmd-9-1937-2016

Faraone FP, Melfi R, Di Nicola MR, Giacalone G, Valvo ML (2020) Phylogenetic relationships of the Italian populations of Horseshoe Whip snake *Hemorrhois hippocrepis* (Serpentes, Colubridae). Acta Herpetologica 15(2): 129–135. https://doi.org/10.13128/a_h-9058

Franklin J (2009) Mapping species distributions. Ecology, biodiversity and conservation. Cambridge University Press, Cambridge, 320 pp. https://doi.org/10.1017/CBO9780511810602

Gavrilets S, Li H, Vose MD (2000) Patterns of parapatric speciation. Evolution 54(4): 1126–1134. https://doi.org/10.1111/j.0014-3820.2000.tb00548.x

GBIF (2024) GBIF Occurrence Download. https://doi.org/10.15468/dl.6jkmk9

Gomes VHF, IJff SD, Raes N, Amaral IL, Salomão RP, de Souza Coelho L, et al. (2018) Species Distribution Modelling: Contrasting presence-only models with plot abundance data. Scientific Reports 8(1): 1003. https://doi.org/10.1038/s41598-017-18927-1

Guisan A, Thuiller W, Zimmermann NE (2018) Habitat suitability and distribution models: with applications in R. Cambridge University Press, 477 pp. https://doi.org/10.1017/9781139028271

Gül S (2019) Is there an ecological barrier between allopatric spotted newts (*Neurergus strauchii* and *Neurergus crocatus*) in Turkey? A view to the glacier mountains of Hakkari. In: Salamanders: Habitat, Behavior and Evolution. Nova Science Publishers, New York, 63–83.

Hurvich CM, Tsai C-L (1989) Regression and time series model selection in small samples. Biometrika 76(2): 297–307. https://doi.org/10.1093/biomet/76.2.297

iNaturalist (2025) Observations of *Hemorrhois* species. https://www.inaturalist.org [on 4 January 2025]

Jablonski D, Mebert K, Masroor R, Simonov E, Kukushkin O, Abduraupov T, Hofmann S (2024) The Silk roads: Phylogeography of Central Asian dice snakes (Serpentes: Natricidae) shaped by rivers in deserts and mountain valleys. Current Zoology 70(2): 150–162. https://doi.org/10.1093/cz/zoad008

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at

high resolution for the earth's land surface areas. Scientific Data 4: 170122. https://doi.org/10.1038/sdata.2017.122

Kazemi SM, Jahan-Mahin MH, Mohammadian-Kalat T, Hosseinzadeh MS, Weinstein SA (2023) Local envenoming by the coinsnake or Asian racer, *Hemorrhois nummifer* and mountain racer or leopard snake, *Hemorrhois ravergieri* (Serpentes: Colubridae, Colubrinae) in Iran: a reminder of the importance of species identification in the medical management of snakebites. Toxicon 226: 107070. https://doi.org/10.1016/j.toxicon.2023.107070

Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12: 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Li Y, Wang Y, Zhao C, Du X, He P, Meng F (2024) Predicting the spatial distribution of three *Ephedra* species under climate change using the MaxEnt model. Heliyon 10: e32696. https://doi.org/10.1016/j.heliyon.2024.e32696

Liz AV, Rödder D, Gonçalves DV, Velo-Antón G, Fonseca MM, Geniez P, ..., Brito JC (2021) The role of Sahara highlands in the diversification and desert colonization of the Bosc's fringe-toed lizard. Journal of Biogeography 48(11): 2891–2906. https://doi.org/10.1111/jbi.14250

Luiselli L, Capula M, Rugiero L, Salvi D, Akani GC (2012) Does interspecific competition with a stronger competitor explain the rarity of an endangered snake on a Mediterranean island? Ecological Research 27(3): 649–655. https://doi.org/10.1007/s11284-012-0936-6

Luna S, Peña-Peniche A, Mendoza-Alfaro R (2024) Species distribution model accuracy is strongly influenced by the choice of calibration area. Biodiversity Informatics 18: 43–55. https://doi.org/10.17161/bi.v18i.22655

Machado L, Harris DJ, Salvi D (2021) Biogeographic and demographic history of the Mediterranean snakes *Malpolon monspessulanus* and *Hemorrhois hippocrepis* across the Strait of Gibraltar. BMC Ecology and Evolution 21: 210. https://doi.org/10.1186/s12862-021-01941-3

Mammola S, Arnedo MA, Pantini P, Piano E, Chiappetta N, Isaia M (2018) Ecological speciation in darkness? Spatial niche partitioning in sibling subterranean spiders (Araneae: Linyphiidae: Troglohyphantes). Invertebrate Systematics 32(5): 1069–1082.

Manel S, Williams HC, Ormerod SJ (2001) Evaluating presence–absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38(5): 921–931. https://doi.org/10.1046/j.1365-2664.2001.00647.x

McCormack JE, Zellmer AJ, Knowles LL (2010) Does niche divergence accompany allopatric divergence in *Aphelocoma* jays as predicted under ecological speciation?: Insights from tests with niche models. Evolution 64(5): 1231–1244. https://doi.org/10.1111/j.1558-5646.2009.00900.x

Montes E, Feriche M, Alaminos E, Pleguezuelos JM (2020a) The Horseshoe whip snake (*Hemorrhois hippocrepis*) on Ibiza: predator release in an invasive population. Amphibia-Reptilia 42(2): 249–254. https://doi.org/10.1163/15685381-bja10039

Montes E, Feriche M, Ruiz-Sueiro L, Alaminos E, Pleguezuelos JM (2020b) Reproduction ecology of the recently invasive snake *Hemorrhois hippocrepis* on the island of Ibiza. Current Zoology 66(4): 363–371. https://doi.org/10.1093/cz/zoz059

Montes E, Gallo-Barneto R, Cabrera-Pérez MÁ (2021) Presence of the horseshoe whip snake (*Hemorrhois hippocrepis*) on Gran Canaria, Spain. Boletín de la Asociación Herpetológica Española 32(1): 97–100.

Morales-Castilla I, Olalla-Tárraga MÁ, Bini LM, De Marco Jr P, Hawkins BA, Rodríguez MÁ (2011) Niche conservatism and species richness patterns of squamate reptiles in eastern and southern Africa: Squamate richness patterns in Africa. Austral Ecology 36(5): 550–558. https://doi.org/10.1111/j.1442-9993.2010.02186.x

Muscarella R, Galante PJ, Soley-Guardia M, Boria RA, Kass JM, Uriarte M, Anderson RP (2014) ENM eval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution 5(11): 1198–1205. https://doi.org/10.1111/2041-210X.12261

Nakazato T, Warren DL, Moyle LC (2010) Ecological and geographic modes of species divergence in wild tomatoes. American Journal of Botany 97(4): 680–693. https://doi.org/10.3732/ajb.0900216

Nunes LA, Raxworthy CJ, Pearson RG (2022) Evidence for ecological processes driving speciation among endemic lizards of Madagascar. Evolution 76(1): 58–69. https://doi.org/10.1111/evo.14409

Pearson RG (2007) Species' distribution modeling for conservation educators and practitioners. Synthesis. Lessons in Conservation 3: 54–89. https://doi.org/10.5531/cbc.linc.3.1.3

Pelegrin N, Winemiller KO, Vitt LJ, Fitzgerald DB, Pianka ER (2021) How do lizard niches conserve, diverge or converge? Further exploration of saurian evolutionary ecology. BMC Ecology and Evolution 21: 1–13. https://doi.org/10.1186/s12862-021-01877-8

Peterson AT, Papeş M, Soberón J (2008) Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213(1): 63–72. https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson AT, Soberón J, Pearson RG, Anderson RP, Martínez-Meyer E, Nakamura M, Araújo MB (2011) Ecological niches and geographic distributions (MPB-49). Princeton University Press, 328 pp. https://doi.org/10.23943/princeton/9780691136868.001.0001

Peterson AT, Papeş M, Soberón J (2015) Mechanistic and correlative models of ecological niches. European Journal of Ecology 1(2): 28–38. https://doi.org/10.1515/eje-2015-0014

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31(2): 161–175. https://doi.org/10.1111/j.0906-7590.2008.5203.x

Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2009) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19(1): 181–197. https://doi.org/10.1890/07-2153.1

Pleguezuelos JM, Feriche M (2002) *Coluber hippocrepis* Linnaeus, 1758. Culebra de herradura. In: Pleguezuelos JM, Márquez R, Lizana M (Eds) Atlas y libro rojo de los anfibios y reptiles de España, AHE-MMA, Madrid, 266–268.

Pomara LY, LeDee OE, Martin KJ, Zuckerberg B (2014) Demographic consequences of climate change and land cover help explain a history of extirpations and range contraction in a declining snake species. Global Change Biology 20(7): 2087–2099. https://doi.org/10.1111/gcb.12510

QGIS.org (2025). QGIS Geographic Information System. Open Source Geospatial Foundation Project; QGIS Association, Switzerland. http://www.qgis.org

R Core Team (2024) R: A language and environment for statistical computing, R foundation for statistical computing, Vienna. https://www.r-project.org/

Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distributions: complexity, overfitting and evaluation. Journal of Biogeography 41(4): 629–643. https://doi.org/10.1111/jbi.12227

Rato C, Harris DJ, Perera A, Carvalho SB, Carretero MA, Rödder D (2015) A combination of divergence and conservatism in the niche evolution of the Moorish gecko, *Tarentola mauritanica* (Gekkota: Phyllodactylidae). PLoS ONE 10(5): e0127980. https://doi.org/10.1371/journal.pone.0127980

Rodríguez-Ruiz R, Juárez-Agis A, García-Sánchez S, Olivier-Salome B, Zeferino-Torres J, Rivas-González M (2020) Modelling the current and future potential distribution of *Maconellicoccus hirsutus* (Green, 1908) a pest of importance for Mexico. Agro Productividad 13(8): 47–52. https://doi.org/10.32854/agrop.vi.1653

Romero-Iraola I, Freitas I, Jiménez-Ruíz Y, Geniez P, García-París M, Martínez-Freiría F (2023) Phylogeographic and paleoclimatic modelling tools improve our understanding of the biogeographic history of *Hierophis viridiflavus* (Colubridae). Animals 13(13): 2143. https://doi.org/10.3390/ani13132143

Salvi D, Mendes J, Carranza S, Harris DJ (2018) Evolution, biogeography and systematics of the western Palaearctic *Zamenis* ratsnakes. Zoologica Scripta 47(4): 441–461. https://doi.org/10.1111/zsc.12295

Sexton JP, McIntyre PJ, Angert AL, Rice KJ (2009) Evolution and ecology of species range limits. Annual Review of Ecology, Evolution and Systematics 40: 415–436. https://doi.org/10.1146/annurev.ecolsys.110308.120317

Soberon J, Peterson AT (2005) Interpretation of models of fundamental ecological niches and species' distributional areas. Biodiversity Informatics 2: 1–10. https://doi.org/10.17161/bi.v2i0.4

Sun C, Zhu L, Liu Y, Wei T, Guo Z (2022) CMIP6 model simulation of concurrent continental warming holes in Eurasia and North America since 1990 and their relation to the Indo-Pacific SST warming. Global and Planetary Change 213: 103824. https://doi.org/10.1016/j.gloplacha.2022.103824

Şahin MK, Candan K, Karakasi D, Lymberakis P, Poulakakis N, Kumlutaş Y, Yildirim E, Ilgaz Ç (2022) Ecological niche differentiation in the Anatolian rock lizards (Genus: *Anatololacerta*) (Reptilia: Lacertidae) of the Anatolian Peninsula and Aegean Islands. Acta Herpetologica 17(2): 165–175. https://doi.org/10.36253/a_h-13089

Şahin MK (2024) The potential range and future distribution of the endangered lizard *Darevskia clarkorum* in the Caucasus Biodiversity Hotspot under climate change scenarios. Zoology in the Middle East 70(1): 1–11. https://doi.org/10.1080/09397140.2024.2314338

Vaissi S, Kurnaz M, Şahin MK, Hernandez A (2023) Climatic niche divergence and conservatism promote speciation in snake-eyed skinks (Sauria: Scincidae): New insight into the evolution and diversification of *Ablepharus* species. Evolutionary Biology 50(2): 249–263. https://doi.org/10.1007/s11692-023-09603-6

Vaissi S, Mohammadi A (2024) Climate-driven distribution shifts of Iranian amphibians and identification of refugia and hotspots for effective conservation. Scientific Reports 14(1): 31610. https://doi.org/10.1038/s41598-024-79293-3

Vaissi S, Şahin MK, Kurnaz M (2024) Niche dynamics and climate change sensitivity in western Palearctic *Zamenis* ratsnakes (Reptilia: Colubridae). Amphibia-Reptilia 46(1): 33–50. https://doi.org/10.1163/15685381-bja10209

Veverková B (2021) Ecological effects of climate change on snakes. Bachelor Thesis, Charles University, Prague, Czechia.

Warren DL, Matzke NJ, Cardillo M, Baumgartner JB, Beaumont LJ, Turelli M, Glor RE, Huron NA, Simões M, Iglesias TL, Piquet JC, Dinnage R (2021) ENMTools 1.0: an R package for comparative ecological biogeography. Ecography 44(4): 504–511. https://doi.org/10.1111/ecog.05485

Wiens JJ (2011) The niche, biogeography and species interactions. Philosophical Transactions of the Royal Society B: Biological Sciences 366: 2336–2350. https://doi.org/10.1098/rstb.2011.0059

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36(1): 519–539. https://doi.org/10.1146/annurev.ecolsys.36.102803.095431

Winter M, Fiedler W, Hochachka WM, Koehncke A, Meiri S, De La Riva I (2016) Patterns and biases in climate change research on amphibians and reptiles: a systematic review. Royal Society Open Science 3(9): 160158. https://doi.org/10.1098/rsos.160158

Supplementary material 1

Raw species occurrence records of *Hemorrhois* species from literature, online source databases, and personal trips

Author: Mehmet Kürşat Şahin

Data type: docx

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl1

Supplementary material 2

Mobility-Oriented Parity (MOP) analysis for projected distribution of *Hemorrhois algirus* under future climate conditions

Author: Mehmet Kürşat Şahin

Data type: tiff

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl2

Supplementary material 3

Mobility-Oriented Parity (MOP) analysis for projected distribution of *Hemorrhois hippocrepis* under future climate conditions

Author: Mehmet Kürşat Şahin
Data type: tiff
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl3

Supplementary material 4

Mobility-Oriented Parity (MOP) analysis for projected distribution of *Hemorrhois nummifer* under future climate conditions

Author: Mehmet Kürşat Şahin
Data type: tiff
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl4

Supplementary material 5

Mobility-Oriented Parity (MOP) analysis for projected distribution of *Hemorrhois ravergieri* under future climate conditions

Author: Mehmet Kürşat Şahin
Data type: tiff
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl5

Supplementary material 6

Species range change (SRC) of *Hemorrhois* species in recently suitable habitats

Author: Mehmet Kürşat Şahin
Data type: tiff
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl6

Supplementary material 7

Results of identity tests for each *Hemorrhois* species

Author: Mehmet Kürşat Şahin
Data type: tiff
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl7

Supplementary material 8

Results of asymmetric and symmetric background similarity tests for each parapatric *Hemorrhois* species

Author: Mehmet Kürşat Şahin
Data type: tiff
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.
Link: https://doi.org/10.3897/herpetozoa.38.e151017.suppl8